NEUROSECRETION. XI. THE EFFECTS OF NERVE SECTION ON THE INTERCEREBRALIS-CARDIACUM-ALLATUM SYSTEM OF THE INSECT LEUCOPHAEA MADERAE [1]

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In the course of a histological study of the intercerebralis-cardiacum-allatum system in specimens of the insect *Leucophaea maderae* in which the nervi corporis cardiaci had been sectioned (B. Scharrer, 1946a), it became evident that this system offers a favorable material for the investigation of a question of general importance, namely that of the transport of neurosecretory material along nerve fibers.

The intercerebralis-cardiacum-allatum system of insects is in many ways analogous to the hypothalamo-hypophyseal system of vertebrates (Hanström, 1941; M. Thomsen, 1943; Scharrer and Scharrer, 1944; Cazal, 1948). In both cases histological observations suggest that the stainable material produced by the neurosecretory cells of the pars intercerebralis and the hypothalamus, respectively, passes along the axons of these cells into organs in which it is stored. In the insects these axons form the nervi corporis cardiaci (nervi corporis cardiaci I, Hanström) and reach not only the corpora cardiaca but in part also the corpora allata. The corpora cardiaca act in the capacity of storage organs for neurosecretory material, in at least a number of species (B. Scharrer, 1951; 1952c); in the vertebrates the neurohypophysis fulfills a corresponding function (Bargmann and Scharrer, 1951).

If the neurosecretory substance actually "migrates" along the axons of the cells from which it originates, it might accumulate when its flow is blocked, as for instance by section of the nerve fibers. Hild (1951), working with frogs, and Stutinsky (1951), using frogs and rats, were indeed able to demonstrate the accumulation of neurosecretory material in the pituitary stalk proximal to the site of section. Scharrer and Wittenstein (1952) reported corresponding observations in dogs in which the pituitary stalk had been severed. However, when compared with insects, vertebrates do not offer equally favorable conditions for the study of this problem. In the operation on vertebrates not only nerve fibers, but also blood vessels must, by necessity, be severed. It is difficult to assess the part played by the interruption of the vascular channels in causing histological changes in addition to those following the severance of the nerve fibers. In the intercerebralis-cardiacum-allatum system of insects the effect of the interruption of the fiber tracts can be studied without reference to changes that might be caused by interference with the blood supply. A further advantage is that the intercerebralis-cardiacum-allatum system is paired in many insects, including Leucophaea. Consequently, the neurosecretory pathway can be sectioned on one side without damage to the other side which serves as control in the same animal. The effects of the interruption of this neurosecretory

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pathway were studied, therefore, in Leucophaea with regard to (a) the transport of the stainable material produced by neurosecretory cells along the axons of these cells, (b) the storage function of the corpora cardiaca, and (c) the reaction of the corpora allata.

Material and Methods

Nerve sections were performed in 124 nymphs and in 115 adults of Leucophaea of both sexes. The nervi corporis cardiaci which enter the corpora cardiaca soon after emerging from the postero-ventral surface of the brain are not easily accessible. The most suitable approach was found to be through a window cut anteriorly in the head capsule; the brain had to be somewhat tilted so that the nerves could be severed. As a rule the operation was performed in nymphs at the beginning of an intermolt period and in adults shortly after emergence. The operated specimens were allowed to survive from 5 days to 10 months. The heads were fixed in Zenker-formol or Bouin, and serial sections of 5 micra were stained with Gomori's (1941) chrome alum-hematoxylin-phloxin method or with Foot's (1933) modification of Masson's trichrome stain. While the Gomori technique is not more specific for the identification of neurosecretory material than the Masson method, it affords a more precise characterization of this substance in both vertebrates and invertebrates than the Masson and other previously used methods and is, therefore, preferable. The sections on which the present study is based include cases with unilateral and with bilateral interruption of the nervi corporis cardiaci.

Since the amount of neurosecretory material normally present in the intercerebralis-cardiacum complex varies to some degree with age, physiological conditions, etc., the cases with unilateral nerve section are particularly instructive for the determination of the histological changes resulting from the interruption of the neurosecretory pathway.

Observations

The effects of the severance of the nervi corporis cardiaci on the histological appearance of the intercerebralis-cardiacum-allatum system of Leucophaea are twofold. One result of this operation consists in marked effects on the distribution of the neurosecretory material, the other concerns a structural change in the corpora allata. Male and female animals respond to the operation in the same manner.

The topography of the organs in question as well as the levels at which sections for photomicrographs (Figs. 2–9) were selected are indicated diagrammatically in Figure 1. The paired nervi corporis cardiaci which originate from the neurosecretory cells of the pars intercerebralis cross before leaving the brain. Their axons enter the elongated corpora cardiaca where they can be traced on each side for a considerable distance as a well defined nerve bundle. In all probability some of the fibers reach the corpora allata, but since in Leucophaea the corpora allata are directly attached to the posterior end of the corpora cardiaca, there is no distinct nervus corporis allati.

As has been pointed out previously (Scharrer and Scharrer, 1944) the distinctive feature of the nervous pathway connecting the pars intercerebralis of the brain with the corpora cardiaca-allata is the presence of varying amounts of neurosecretory material throughout its course. Within the corpus cardiacum this material, which stains deep blue with the Gomori technique and bright red with the Masson stain,

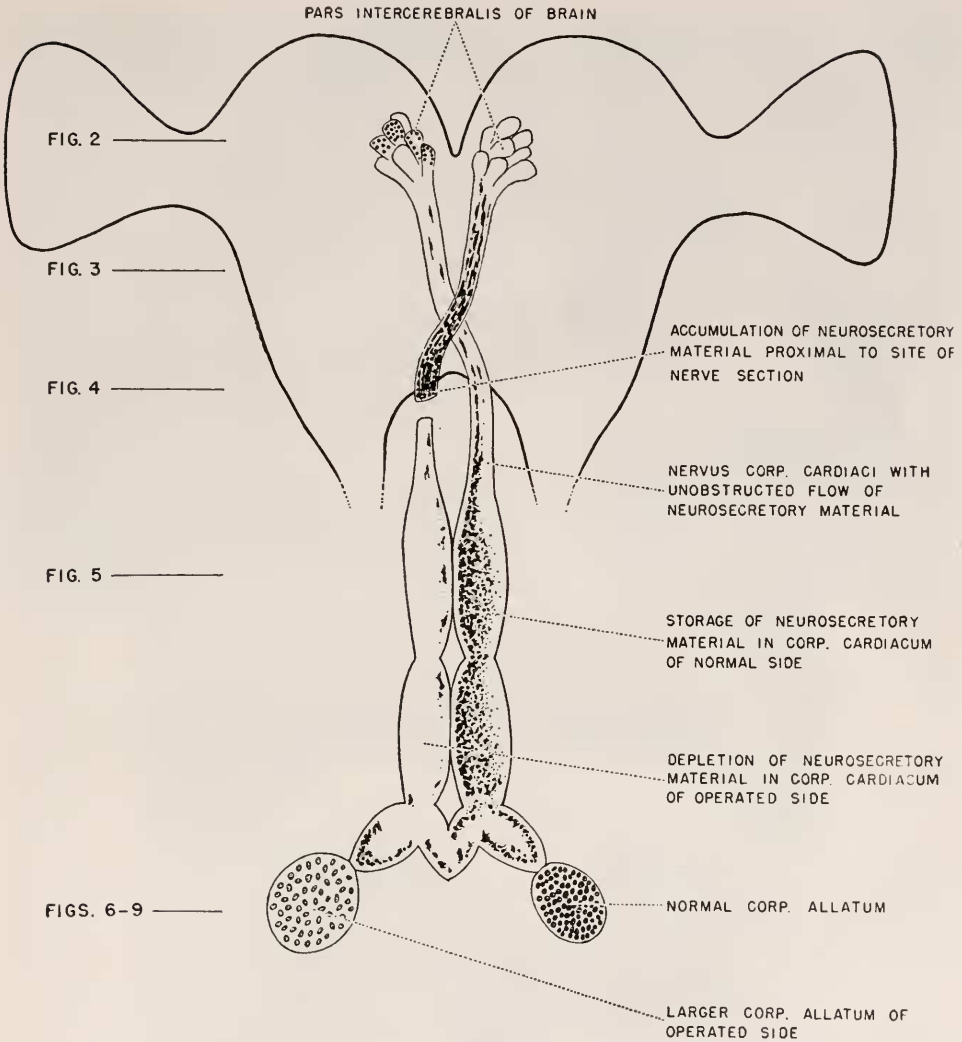


FIGURE 1. Diagram of the dorsal aspect of the intercerebralis-cardiacum-allatum system of *Leucophaea maderae*. On the left side the nervus corporis cardiaci is severed with the result that neurosecretory material is increased proximal to and depleted distal to the site of nerve section. On the operated side the corpus cardiacum is decreased, the corpus allatum increased in size. Levels of the photomicrographs shown in Figures 2–9 are indicated; the sections illustrated in these figures were made from paraffin-embedded material, cut at 5 micra, and stained with the chrome alum-hematoxylin-phloxin method of Gomori.

follows in its distribution the course of the fiber bundles of the nervi corporis cardiaci. This topographic relationship is particularly evident in the anterior portion of the corpora cardiaca. Masses of neurosecretory material are usually confined to this nerve bundle for some distance and, farther distally, "fan out" into the cardiacum tissue. Neurosecretory material is, as a rule, more abundant in the marginal zones,

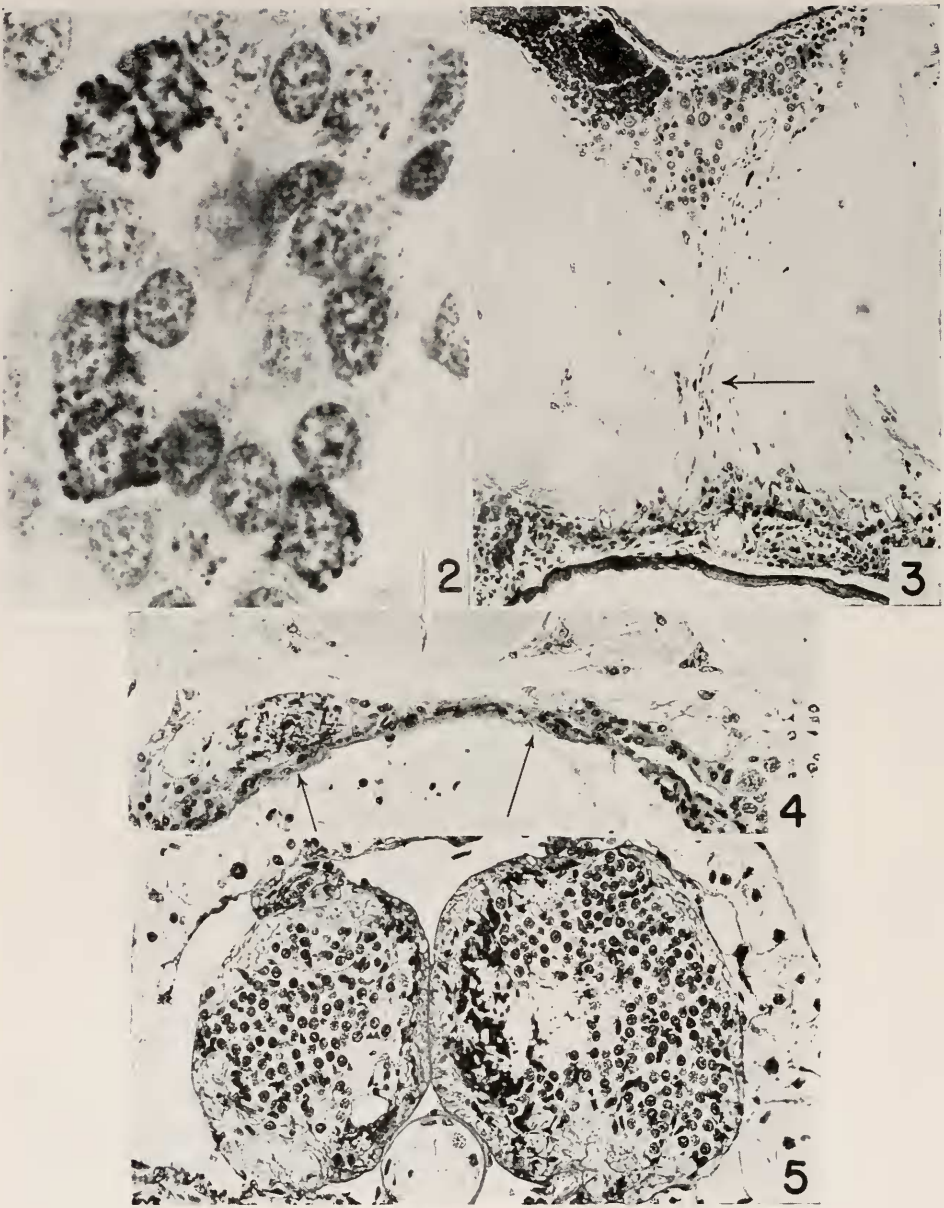


FIGURE 2. Neurosecretory cells of the pars intercerebralis of Leucophaea on the unoperated side with conspicuous cytoplasmic inclusions. The operated side of this case shows very little neurosecretion. Adult female, fixed in Bouin 5½ months after operation. Photomicrograph, × 1000.

FIGURE 3. Brain of adult female fixed in Bouin five months after operation. Level of decussation of nervi corporis cardiaci. At the arrow the tract of the operated side, which contains an increased amount of dark staining neurosecretory material, crosses the almost empty tract of the intact side (compare with Figure 1). Photomicrograph, × 100.

particularly those facing the lumen of the dorsal vessel which is surrounded by the corpora cardiaca. In the same sections the corpora allata are free of neurosecretory substance.

I. *The effect of the severance of the nervi corporis cardiaci on the distribution of neurosecretory material*

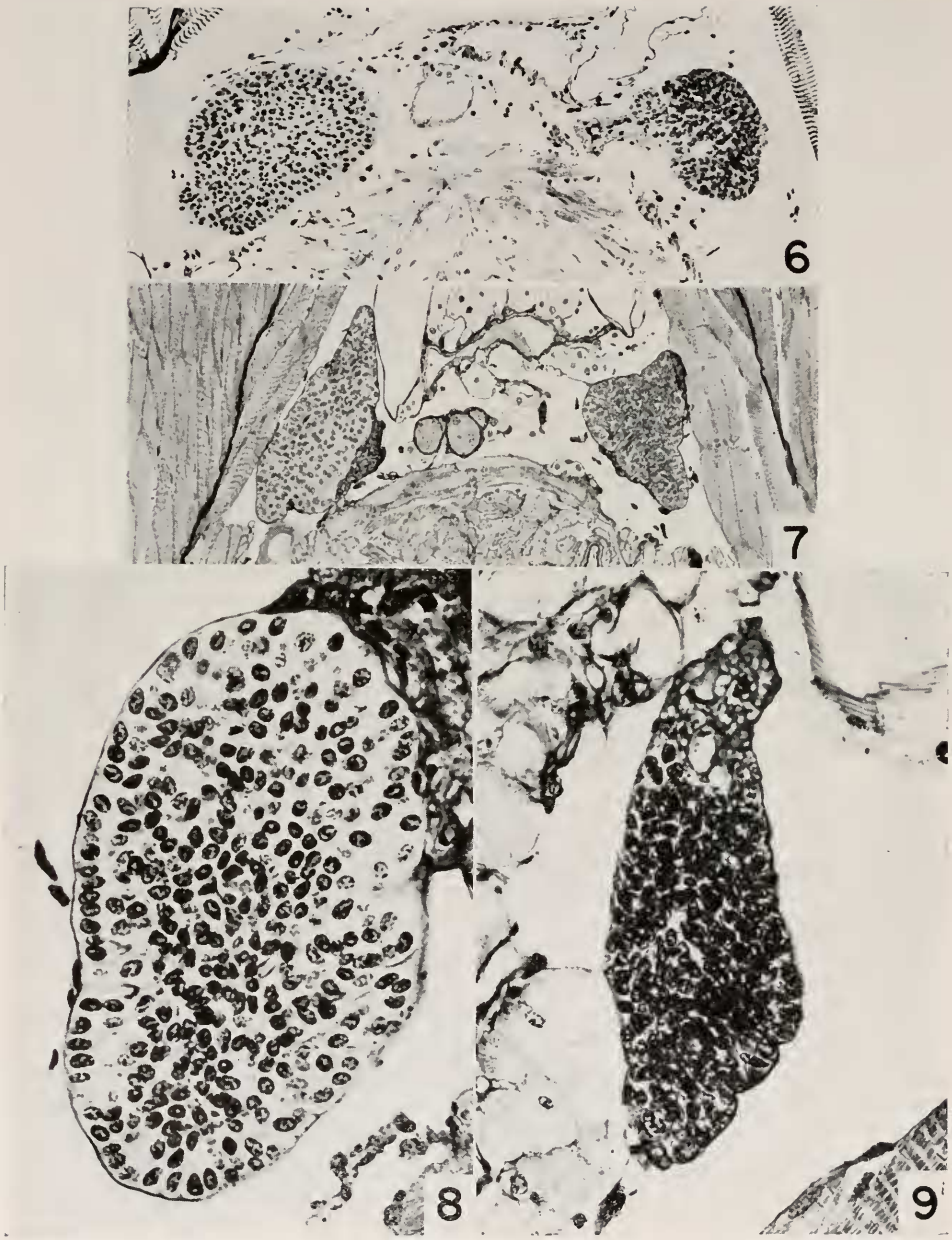
If the neurosecretory pathway is interrupted in the manner described, the result is an accumulation of neurosecretory material proximal to the site of operation and a marked depletion of this substance in the distal portions of this system (B. Scharrer, 1952a). These histological changes suggest that the normally occurring flow of neurosecretory material along the axons of the cells in which it originates must have been blocked by the nerve section.

The accumulation of neurosecretory material at the proximal end of the cut fiber tract is particularly noticed in cases where the interval between the operation and the fixation of the tissues is short, *i.e.*, several days. Figure 4 shows a cross section through the nervi corporis cardiaci near the ventral surface of the brain a short distance from their exit. On the side where the operation was performed the nerve contains considerable masses of neurosecretory material, while the nerve on the unoperated side contains only a small amount. In cases where the interval between the operation and the fixation of the organs is several months, the accumulated neurosecretory substance usually extends to a more proximal point with the result that the severed tract, throughout its course within the brain, shows an increased amount of inclusions as compared with the control side (Fig. 3). This phenomenon of accumulation of the substance is also observed in cases of bilateral nerve section which serve to corroborate the results of unilateral operations. In specimens which had been allowed to survive for the longest period of time in this series of experiments (up to 10 months) the accumulation effect may be absent. It is to be assumed that the neurosecretory cells whose axons have been cut eventually cease to produce, or produce a smaller amount of the material which is normally transported to the corpora cardiaca. This assumption is supported by the observation that in some of the long interval cases studied the cells of the pars intercerebralis contain more neurosecretory material on the normal than on the operated side (Fig. 2).

While the section of the nervi corporis cardiaci results in an increase of neurosecretory material in the proximal part of the system, the portions distal to the level of transection show a reduction in the amount of this substance. Figure 5 demonstrates the difference between normal and operated side in that the corpus cardiacum whose nerve has been severed contains practically no material stainable with the

FIGURE 4. Cross section of nervi corporis cardiaci (arrows) in postero-ventral part of brain near site of their emergence. The severed tract on the left side, shown proximal to the level of operation, contains considerably more dark staining material than the intact tract on the right side. Female fixed in Zenker-formol five days after nerve severance. Photomicrograph, × 160.

FIGURE 5. Cross section of corpora cardiaca of female with unilateral severance of nervus corporis cardiaci, operated five months before fixation in Bouin. The corpus cardiacum on the operated (left) side is smaller and contains very little neurosecretory material in contrast to the normal control gland on the right side which shows dark masses of this substance in the medial zone. Photomicrograph, × 210.



FIGURES 6–9. Corpora allata of Leucophaea with unilateral severance of the nervus corporis cardiaci. The organs on the operated side at left are "swollen" with more cytoplasm and looser arrangement of nuclei than those on the normal right side. Figure 6: Female fixed in Zenker-formol five days after nerve severance. Photomicrograph, × 100. Figure 7: Female fixed in Bouin five months after nerve severance. Photomicrograph, × 100. Figures 8 and 9: Male fixed in Bouin six months after operation. The contrast between "severed" (Fig. 8) and normal (Fig. 9) corpus allatum is particularly marked. Photomicrograph, × 375.

Gomori technique. It also shows that the corpus cardiacum on the operated side is smaller than on the normal side. This effect of nerve severance on the corpus cardiacum is different from that observed on the corpus allatum (see below) and may be the result of prolonged inactivity as a storage center. The posterior part of the corpora cardiaca of specimens with unilateral operation may contain neurosecretory substance on both sides, but since the organs are continuous at the posterior end the material on the operated side probably is derived from the intact side.

II. *The effect of the severance of the nervi corporis cardiaci on the structure of the corpora allata*

In histological preparations, the corpora allata of normal specimens of Leucophaea are, as a rule, conspicuous by the density of their nuclei which make the stained organs look dark. After severance of the nervi corporis cardiaci the histological appearance of the corpora allata changes markedly. The organs appear larger and lighter in color. This effect is brought about by an increase in cytoplasm relative to the number of nuclei per unit of area. The nuclei are especially loosely arranged in the periphery of these organs. It seems that the number of nuclei per gland remains the same after nerve severance, and that the increase in organ size constitutes an increase in cytoplasm, which may be due merely to uptake of water or may indicate an actual production of cytoplasmic material. The nuclei also differ from normal ones after nerve severance; in the operated organs they tend to be more vesicular and their nucleoli are more distinct.

The difference between a normal corpus allatum and one whose connection with the brain has been interrupted can be particularly well demonstrated in cases of unilateral nerve severance. The illustrations (Figs. 6 to 9) show organs from animals which had been allowed to survive the operation for five days, five months, and six months respectively. The structural change is already evident a short time after nerve severance; it is especially marked in the case with an interval of six months after the operation.

The size difference between these normal and "severed" corpora allata was roughly estimated in the following manner. In 5 micra serial sections of the organs, camera lucida outline drawings of every fourth section were made. In the case of an imperfect section the one preceding or following it was substituted. The areas in square millimeters were determined planimetrically and the values were added up for each organ measured. The figures for three representative cases were as follows:

		Normal	Operated
Case 737	♀ (int. 5 ds.)	5,954.83 sq. mm.	10,335.46 sq. mm.
Case 424	♀ (int. 5 ms.)	6,148.37 sq. mm.	8,148.37 sq. mm.
Case 465	♂ (int. 6 ms.)	1,122.58 sq. mm.	5,729.02 sq. mm.

The differences between the values for the normal and the operated side indicate a substantial increase in the size of those corpora allata whose nervous connection with the brain had been severed.

Discussion

The observation that the distribution of neurosecretory material in the intercerebralis-cardiacum complex of Leucophaea changes in the manner described after

the nervi corporis cardiaci are severed, clearly indicates that normally a transport of this material takes place along the axons of the neurosecretory neurons. This conclusion is further supported by the corresponding data in vertebrates as stated in the introduction. In frogs (Hild, 1951), in rats (Stutinsky, 1951) and in dogs (Scharrer and Wittenstein, 1952) the accumulation of neurosecretory material proximal to the site of severance of the pituitary stalk is evident soon (several days) after the operation and disappears after a longer interval. The same is true in Leucophaea. A depletion of this material in the portion distal to the transection, such as that observed in Leucophaea, has so far not been clearly demonstrated in vertebrates, but attention should be called to the fact that the observation of such quantitative differences is more difficult in animals where the organ system in question is unpaired and consequently no comparison can be made with a control organ in the same animal.

As far as other insects are concerned, a comparable transport of neurosecretory material from the brain to the corpus cardiacum must be assumed to take place in a variety of species where, as in Leucophaea, the occurrence of this material in the nervi corporis cardiaci can be demonstrated (Cazal, 1948; Stutinsky, 1952).

The concept of the transport and storage of neurosecretory material in the corpus cardiacum makes understandable the physiological result observed in Leucophaea after the interruption of the nervi corporis cardiaci (B. Scharrer, 1946a). These experiments gave no indication of an acute hormone deficiency and no deficiency should be expected since the operation does not result in the immediate depletion of neurosecretory material in the components of the system. The extent to which the evaluation of the corpus cardiacum as a reservoir for hormones originating in the brain can explain other known physiological observations has been discussed in some detail elsewhere (B. Scharrer, 1952b, 1952c).

The interpretation of the hypothalamo-hypophyseal system of vertebrates (Bargmann and Scharrer, 1951) and of the intercerebralis-cardiacum-allatum system of insects (B. Scharrer, 1951; 1952b; see also Scharrer and Scharrer, 1944) in this new light has led to a re-examination of a comparable situation in the eyestalk of crustaceans. In this group of arthropods the sinus gland has long been considered as the source of a number of hormones, while the functional role of the X organ remained obscure ever since its discovery by Hanström (1931). Recent investigations show that hormones known to be present in the sinus gland, especially the molt-inhibiting hormone, are only stored there; they actually originate in the neurosecretory cells of the X organ from which they are transported to their reservoir via the sinus gland nerve (Passano, 1951a, 1951b; Bliss, 1951; Travis, 1951; Frost, Saloum and Kleinholz, 1951).

Morphological evidence of the presence of neurosecretory material in this nerve has been obtained in a number of brachyurans (Enami, 1951; Bliss, 1951; Passano, 1951a). Nerve section in crustaceans (Passano, 1951a) seems to have an effect on the distribution of the neurosecretory material comparable to that in insects as reported here. The information available now is sufficient proof for the existence of a third neurosecretory system (X organ-sinus gland system) which corresponds in many details to the neurosecretory systems in insects and in vertebrates.

As to the effect of nerve section on the corpora allata, one may inquire into the nature of the structural changes observed in these organs after their connection

with the brain has been severed. Do they represent a specific reaction attributable to the absence of nervous or of endocrine (neurosecretory) stimulation and, if this is so, does the histological response to this operation reflect a change in the physiological activity of the corpora allata?

The reaction to the severance of the nervi corporis cardiaci cannot be explained as an unspecific effect, possibly brought about by the surgical procedure, because if this were true unilateral transection would have to affect both corpora allata in a similar way. Whether the interruption of the nerves in itself or the disturbance in the flow of neurosecretory substance along these nerves causes the change, cannot be decided at this time. There is information, however, regarding the physiological activity of "severed" corpora allata. It has been previously reported (B. Scharrer, 1946a) that the separation from the brain does not render the corpora allata of Leucophaea functionally incompetent. Bilateral section of the nervi corporis cardiaci neither prevents egg maturation nor nymphal molting, both being processes governed by corpus allatum hormone. This result is not unexpected in view of the fact that allatum implants can substitute for the intact gland in allatectomized animals (B. Scharrer, 1946b, 1946c). In these cases the isolated corpora allata react like intact glands, *i.e.*, they furnish hormone which reaches the circulation in sufficient amounts to be effective.

A physiological difference between normal and "severed" organs which may concern hormone release rather than hormone production can be observed in last instar nymphs. It is generally assumed that, in the course of insect development, metamorphosis takes place because the corpora allata in the last larval stage no longer release an adequate amount of juvenile hormone. The manner in which this presumed restraining influence on the corpora allata is mediated has not been determined. The effect of the cutting of the nervi corporis cardiaci shows, however, that this regulatory mechanism requires the intactness of the nervous pathway. Last instars of Leucophaea in which the corpora allata are severed from the brain may undergo supernumerary molts and become "nymphoids" instead of adults (B. Scharrer, 1946a), an indication that the severed corpora allata can release a significant amount of juvenile hormone at a stage when they normally would not do so. This result can be interpreted in several ways. Under normal conditions the brain may regulate the release of corpus allatum hormone by means of the nervi corporis cardiaci. In view of the peculiar nature of this pathway the action on the corpora allata can be either nervous or neuro-endocrine in character. Another possibility is that the potency of the severed corpus allatum is increased to such a degree that the juvenile hormone released during the last stage reaches the threshold necessary for an additional nymphal molt, while normally this level is not reached.

In the latter case the histological changes following nerve severance would have to be interpreted as a sign of increased glandular activity rather than of deficiency. This has been done by some authors who observed structural differences similar to the ones described here in Leucophaea, when they compared the corpora allata of specimens in inactive and active phases of their development (Wigglesworth, 1934; Mendes, 1948), of males and females (Pflugfelder, 1938, 1948; Schrader, 1938; Hanström, 1942; Palm, 1948) or of normal and castrate specimens (Pfeiffer, 1940; E. Thomsen, 1942; Day, 1943; see also Vogt, 1942) of certain insect species.

An effect of nerve severance on the structure of the corpus allatum has been

reported only in one other instance. Day (1943) observed an increase in the size of the corpus allatum comparable to the one in Leucophaea, when the "recurrent" nerve of the fly Sarcophaga was cut. In the adult flies this nerve contains both nervi corporis cardiaci at the level of the operation. Therefore, Day's experiment constitutes a denervation of the corpus allatum, while the severance of the nervi corporis cardiaci in Leucophaea does not deprive the corpora allata of fibers they may receive from the stomatogastric system. Whether or not this anatomical difference, determining different degrees of denervation, accounts for the differences in the physiological effects observed in Leucophaea on the one hand and in Sarcophaga on the other is not certain. While the stimulation of the ovaries of Leucophaea by the corpora allata continues after section of the nervi corporis cardiaci this is not the case in Sarcophaga where, according to Day, nerve severance has the same effect as extirpation of the corpus cardiacum-allatum. With respect to Leucophaea one may assume that the physiological effect which parallels the morphological change of the corpora allata following nerve severance constitutes an increase rather than a decrease in glandular activity.

Summary

1. The interpretation of the intercerebralis-cardiacum-allatum system of insects as a functionally related group of neuroglandular organs, in which the corpus cardiacum serves as a reservoir for neurosecretory material, is supported by the results of severance of the nervi corporis cardiaci. The insect, *Leucophaea maderae*, in which the components of this organ system are paired is favorable for the study of these relationships since one side can be left intact and compared with the operated side.

2. Following the interruption of the neurosecretory pathway at the level where the nervus corporis cardiaci enters the corpus cardiacum, the distribution of the neurosecretory material changes markedly in comparison with the normal situation. Proximal to the site of nerve section there is an accumulation, and distal to it there is a drastic depletion of neurosecretory material. This result offers conclusive evidence that in the intact system the neurosecretory substance originating in cells of the pars intercerebralis of the brain is transported via their axons (forming the nervi corporis cardiaci) to the corpora cardiaca where it is stored. This interpretation of the morphological situation makes it understandable that no physiological indication of hormone deficiency was observed as a consequence of the nerve transection (B. Scharrer, 1946a).

3. Severance of the nervi corporis cardiaci also results in histological changes in the corpora allata. The organs become larger and seem to contain more cytoplasm than normal glands. Their nuclei are more vesicular and the nucleoli more distinct. These changes do not indicate an organ deficiency, since "severed" corpora allata of Leucophaea are functionally equal to, or perhaps even more competent than, normally innervated glands.

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